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DISCOVERY OF A NEW ORNITHOPOD DINOSAUR FROM THE PORTEZUELO FORMATION (UPPER CRETACEOUS), NEUQUÉN, PATAGONIA, ARGENTINA [1]

(With 14 figures)

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ABSTRACT: We describe the postcranial skeleton of a new Cretaceous ornithopod, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. from Patagonia, Argentina. The specimen was found in the Portezuelo Formation, Neuquén Group, Upper Cretaceous. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. is diagnosed by having triradiate sternum with the anterior border tribranched, two laterally placed and outwardly directed, and one centrally placed, smaller, and forwardly directed. Sternal ribs flattened, twisted and distally expanded. Last dorsal vertebra with well-developed hyposphene. A thin plate-like are located in front of the sterna. Together with these autapomorphies, this new species of ornithopod differs from *Talenkauen santacrucensis* by having the pubic peduncle of ilium less developed, a more acute angle between the anterior process of ilium and the pubic peduncle, the acetabular cavity slightly marked. Also present ten cervical vertebrae, fourteen dorsal vertebrae, epipophyses on the third cervical vertebra placed over the distal end of the postzygapophyses and posteriorly projected. The presence of plates on the lateral side of the thorax and well developed epipophyses on the third cervical vertebra, were originally interpreted as autapomorphies for the euiguanodontian *Talenkauen santacrucensis*. These features are also present in *Macrogryphosaurus gondwanicus* gen.nov, sp.nov., and are regarded as synapomorphies defining a new clade of Euiguanodontia dinosaurs comprising the two species: Elasmaria nov.

Key words: *Talenkauen*. Ornithopoda. Elasmaria nov. Portezuelo Formation. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov.

RESUMEN: Hallazgo de un nuevo dinosaurio ornitópodo de la Formación Portezuelo (Cretácico superior) Neuquén, Patagonia, Argentina.

Describimos el esqueleto postcranial de un nuevo ornitópodo Cretácico, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. de Patagonia, Argentina. El especimen fue hallado en la Formación Portezuelo, Grupo Neuquén, Cretácico tardío. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. es diagnosticado por tener un esternón trirradiado con el borde anterior triramificado, dos ramas ubicadas lateralmente y dirigidas hacia afuera, y una ubicada centralmente, pequeña y desplazada hacia adelante. Costillas esternales aplanadas, giradas y distalmente expandidas. Última vértebra dorsal con hipósfeno bien desarrollado. Delgadas placas ubicadas frente al esternón. Junto con estas autapomorfias, esta nueva especie de ornitópodo difiere de *Talenkauen santacrucensis* por tener el pedúnculo púbico del ilion menos desarrollado, un ángulo más agudo entre el proceso anterior del ilion y el pedúnculo púbico, cavidad acetabular levemente marcada. Además, presenta diez vértebras cervicales, catorce vértebras dorsales, epipófisis sobre la tercera vértebra cervical ubicadas sobre el extremo distal de las postzigapófisis y proyectadas posteriormente. La presencia de placas sobre los laterales del tórax y epipófisis bien desarrolladas sobre la tercera cervical fueron originalmente interpretadas como autapomorfías del euiguanodonte *Talenkauen santacrucensis*. Estos caracteres también están presentes en *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. y son considerados sinapomorfías de un nuevo clado de dinosaurios Euiguanodontia: Elasmaria nov., que comprende estas dos especies.

Palabras clave: Talenkauen. Ornithopoda. Elasmaria nov. Formación Portezuelo. *Macrogryphosaurus gondwanicus* gen.nov., sp.nov.

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INTRODUCTION

Among Cretaceous dinosaurs discovered in Argentina, the ornithischians are currently represented by several taxa. Among them are basal ornithopods from Río Negro: *Gasparinisaura cincosaltensis* (Coria & Salgado, 1996; Salgado *et al.*, 1997); Neuquén: *Anabisetia saldiviai* (Coria & Calvo, 2002) and indeterminate ornithopod materials (Porfiri & Calvo, 2002); Chubut: *Notohypsilophodon comodorensis* (Martínez, 1998); and Santa Cruz: *Talenkauen santacrucensis* (novas *et al.*, 2004). Moreover, other ornithischians recorded in this country are the probable ceratopsian *Notoceratops bonarelli* (Tapia, 1918), the Hadrosauridae *Kritosaurus australis* (Bonaparte *et al.*, 1984), probable lambeosaurines (Powell, 1987), and an unnamed nodosaurid ankylosaur (Coria & Salgado, 1996).

During a field trip of the Universidad Nacional del Comahue to Mari Menuco lake in May of 1999, an almost complete and articulated skeleton of an ornithopod was unearthed. The specimen has unusual plates on the thorax. Ornithopods with such feature are uncommon. These plates were recorded in *Thescelosaurus* (Gilmore, 1915) and *Talenkauen* (Novas *et al.*, 2004). Here we describe this new ornithopod dinosaur, which is the biggest non-hadrosaurian ornithopod from South America known up to now. It shares derived characters with the basal euiguanodontian *Talenkauen santacrucensis* (Novas *et al.*, 2004), including the presence of epipophyses on the third cervical, and thin ossified plates on the thorax, suggesting that these two species are closely related, forming a new clade: Elasmaria nov.

Abbreviations: (MUCPv) Museo Universidad Nacional del Comahue, Neuquén, Argentina. (MPM) Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina.

RESULTS

SYSTEMATIC PALEONTOLOGY

Ornithischia Seeley, 1888
Ornithopoda Marsh, 1881
Euornithopoda Sereno, 1986
Iguanodontia Sereno,1986
Euiguanodontia Coria & Salgado, 1996

Elasmaria nov.

Etimology – Elasmaria (Greek), thin plate.

Phylogenetic definition – Elasmaria is phylogenetically defined as *Talenkauen santacrucensis*, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov., their most recent common ancestor plus all the descendants.

Diagnosis – Two unambiguous synapomorphies support the monophyly of Elasmaria: large basal euiguanodontian with well-developed epipophyses on the third cervical and presence of thin ossified plates on thorax.

Macrogryphosaurus gondwanicus gen.nov., sp.nov.

Holotype – MUCPv-321. The specimen was found articulated with the cervical and dorsal series in straight position with the ventral zone upward. Only post-cranial materials are preserved, 8 post-axial cervicals, 14 dorsals, 6 sacrals and 16 caudals, cervical and dorsal ribs, both ilia, pubes, and ischia, one sternum, and 4 thoracic plate.

Etymology – *Macrogryphosaurus,* from Greek m*acro*, big; *grypho*, enigmatic; *saurus*; lizard; and *gondwanicus* in reference to the Gondwana continent.

Locality and horizon – The fossil was found 60 km NW from Neuquén city, on the west coast of the Mari Menuco lake, Neuquén, Argentina. It comes from the Portezuelo Formation (Coniacian), Neuquén Group.

Diagnosis – Triradiate sternum with the anterior border tribranched, two laterally placed and outward directed and one centrally placed smaller and forwardly directed. Sternal ribs flattened, twisted and distally expanded. Last dorsal with well-developed hyposphene. A thin plate-like is located in front of the sterna. Together with these autapomorphies this Elasmarian euiguanodontian differs from *Talenkauen santacrucensis* by having the pubic peduncle of ilium less developed, a more acute angle between the anterior process of ilium and the pubic peduncle, the acetabular cavity slightly marked. Ten cervical vertebrae, fourteen dorsal vertebrae, epipophyses on the 3rd cervical placed over the distal end of the postzygapophyses and posteriorly projected.

DESCRIPTION

We estimate that the holotype specimen of *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. measured no more than 6m long, representing one of the largest known non-hadrosaurian ornithopods yet recorded in South

America. However, the presence of unfused sutures between neural arches and centra in posterior dorsals and proximal caudals suggests that this is probably not a full-grown individual (e.g., GALTON, 1981; SERENO & NOVAS, 1993; BROCHU, 1996). Although the specimen does not preserve cranial and dental elements, which are highly relevant for phylogenetic analysis, the available postcranial bones allow comparisons with other euiguanodontians (e.g., *Gasparinisaura*, *Anabisetia*, *Talenkauen).*

VERTEBRAL COLUMN

The number of presacral and sacral vertebrae in *Macrogryphosaurus* gen.nov. is 10+14+6. Most basal Ornithopoda (e.g., *Heterodontosaurus, Hypsilophodon, Camptosaurus, Talenkauen*) have 9 cervicals, and the number of sacrals is regular in most of them (except for *Camptosaurus*, with 4-5 sacrals). By contrast, the number of dorsals is more variable among these dinosaurs: 12 in *Heterodontosaurus*, 15 in *Hypsilophodon*, 16 in *Talenkauen* and *Camptosaurus*, and 17 in *Iguanodon.*

Thus, *Macrogryphosaurus* is one of the few Ornithopoda with low number of dorsal vertebrae.

Cervical vertebrae: Eight (8) articulated cervicals were found, the lasts 7 are well preserved. We do not have data on atlas and axis. All cervicals (Figs.1-3) have amphicoelous centra; they are wider than high. In lateral view, they have a rectangular shape and in spite of being a little crushed by compression, they are as elongated as in *Talenkauen.* A ventral keel is present from cervical 4th to 8th. Parapophyses are anteriorly placed, and diapophyses are short, rounded, and ventrally projected. In *Talenkauen*, both pre- and postzygapophyses are elongate, extending beyond centrum level. Cervical 3 bears well-developed epipophyses above the postzygapophyses (Fig.1A). This feature, as well as the elongate condition of most cervical centra, are unusual among ornithischian dinosaurs, and are uniquely shared with *Talenkauen* (NOVAS *et al.*, 2004) (Fig.2). *Lesothosaurus* has epipophyses on the third cervical but they are less developed than in *Macrogryphosaurus* and *Talenkauen.* Moreover, this feature in *Macrogryphosaurus* differs from that of *Talenkauen* because, in the former, the epipophyses are posteriorly projected and placed on the distal end of the postzygapophyses.

In the 4th cervical of *Macrogryphosaurus* gen.nov. (Fig.1B), epipophyses are placed on the proximal end of the postzygapophyses, and they are more reduced and different from those of *Talenkauen.* Neural spines in anterior cervicals are short and placed at mid-length of the centra. The neural canal has a circular shape. From cervicals 5 to 10, the anterior face of the centrum is heart-shaped. The diapophyses are directed caudolaterally and ventrally. Anterior neural spines are higher than posterior ones; they are rounded at the distal end and posteriorly directed. Postzygapophyses are elongated, with the articular surfaces slightly concave. In posteriors cervicals, the neural canal has a quadrangular shape and the diapophyses are caudolaterally projected.

Dorsal vertebrae: The dorsal series was found complete, with 14 vertebrae, and articulated. At both sides of vertebrae 13 and 14, ossified tendons have been preserved. All dorsals are slightly

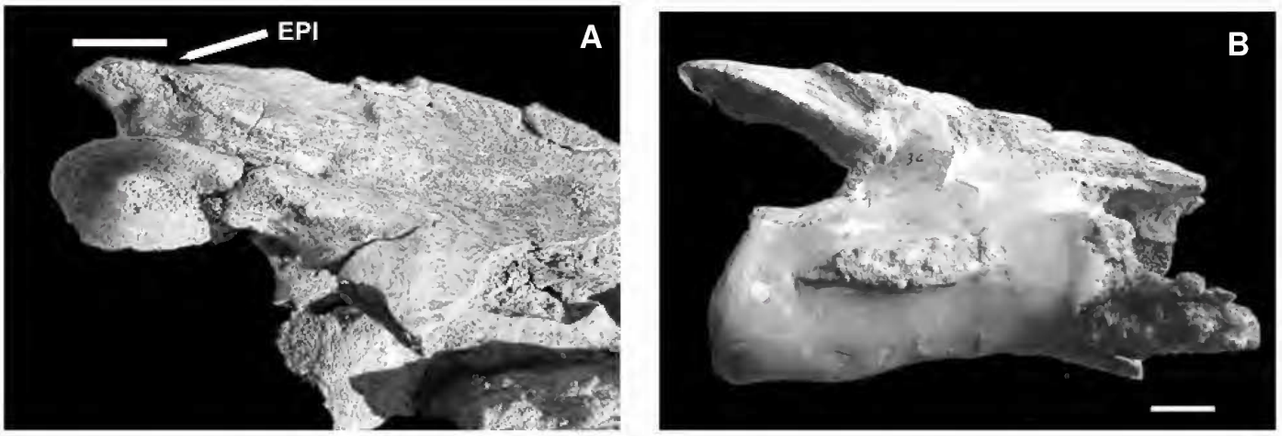


Fig.1- *Macrogryphosaurus gondwanicus* sp.nov. (A-B) third and fourth cervicals in lateral view. Scale bar = 1cm.

amphycoelous. Dorsal 1 is recognized by having the parapophyses on the neurocentral suture. Anterior dorsals have centra transversely compressed, with the ventral surface strongly concave laterally. The parapophyses are small, with oval articular surfaces. Diapophyses are caudally directed. The subcircular and slightly convex articular facets of prezygapophyses are inclined medially 45 degree with respect to the sagittal plane. Neural spines are transversely thin. In dorsal 1, the distal end of the neural spine is rounded, but from dorsal 2 and backwards, it is rectangular-shaped. Centra of posterior dorsals have anterior surfaces slightly smaller than the posterior ones. Ventrally, a keel is present, at least, in dorsals 13 and 14. Its presence on vertebrae 5 to12 is uncertain, because this area is covered by sediments. A pair of foramina is present on both sides of the ventral keel in dorsal 13, but in dorsal 14 both foramina are placed only on the rigth side. Other small foramina are also present on the upper half of the lateral side of the centra. Diapophyses of the posterior dorsals are anterodorsally projected, and parapophyses are small and fused to the proximal part of the diapophyses. The neural canal is small and subcircular. The last dorsal (14^{th}) has a well-developed hyposphene (Fig.4A), a character not documented before in other ornithischian dinosaurs. It is absent in dorsal 13; and in the first sacral, there is no hypantrum.

Caudal vertebrae: 16 caudal vertebrae were found, most of them incomplete, preserving only centra and neural arches, with partial neural spines. All caudal centra are amphyplatian and subcircular in anterior view. Caudal 1 to 3 have a strong hypapophyses. On the lateroventral side of the centra, several foramina are present in these caudals. Two small spinoprezygapophyseal laminae are present. There is a prespinal lamina that reaches the base of the neural arch in caudals 2 and 3. Three anterior neural spines, and two transverse processes without the centra were also recovered. Neural spines are transversely thin and high, and transverse processes are directed backwards. Mid caudals have centra higher than wide. A deep ventral sulcus is present, which becomes less marked in distal caudals. Mid-caudal chevrons are narrowed in lateral view, and slightly curved distally. Contrary to what is observed in mid-caudals, the posterior haemal arches are triangular in lateral view, and have expanded distal ends (Fig.5). Six articulated distal caudals, partially complete, are articulated with their corresponding haemal arches. Neural spines are small, rounded and transversely thin proximally.

Pectoral Girdle

Sternum: The sternum is triradiate; on the anterior border, three branches are present, two laterally placed, and outwardly directed, and one centrally placed, smaller, and forwardly directed (Fig.6). The anterior border is three times wider than the posterior one. Lateral borders are concave.

Sternal ribs: Three sternal ribs were found articulated with the sternum; although four were present originally. They are flattened, twisted and distally expanded.

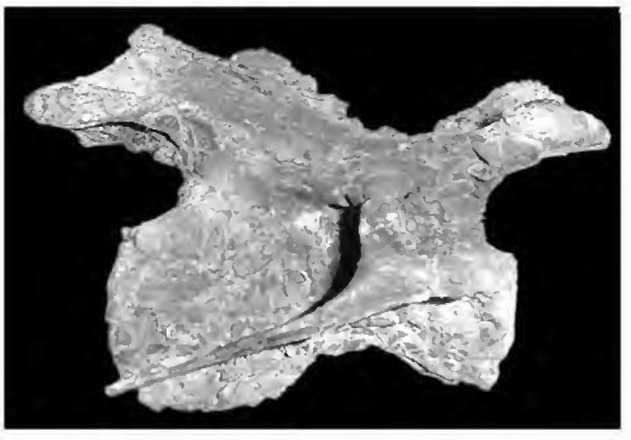


Fig.2- *Talenkauen santacrucensis*. Third cervical in lateral view.

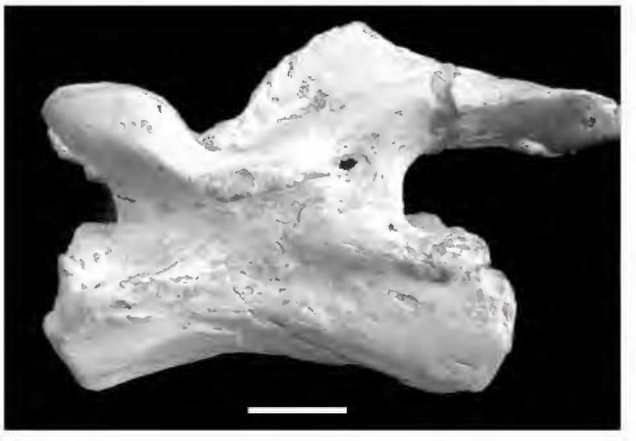


Fig.3- *Macrogryphosaurus gondwanicus* sp.nov. Cervical vertebrae (8^{th}) in lateral view. Scale bar = 1cm.

Fig.4- *Macrogryphosaurus gondwanicus* sp.nov. Dorsal vertebrae (14th) in (A) posterior, and (B) lateral views. Scale bar = 1cm.

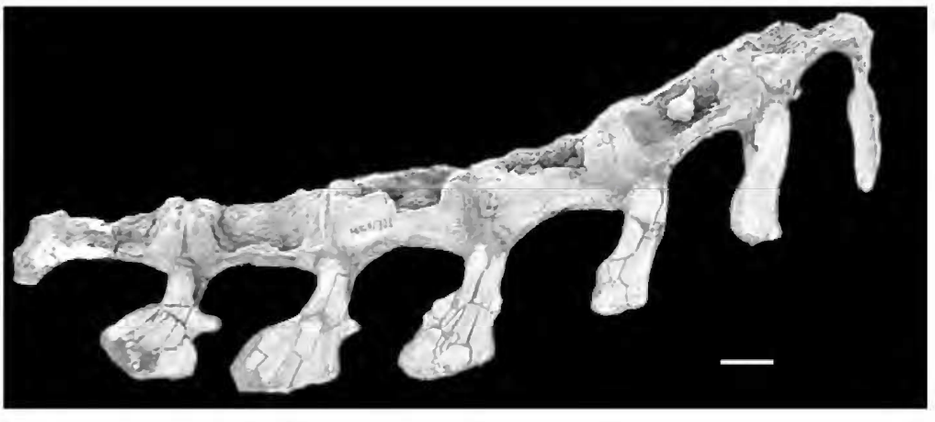


Fig.5- *Macrogryphosaurus gondwanicus* sp.nov. Posterior caudals, in lateral view. Scale bar = 2cm.

Plates: *Macrogryphosaurus* has ossified plates placed along the dorsal region of the thorax, from ribs 6 to 8 (Figs.7-8). These ossifications are subcircular and thin (1 to 3mm thick) and one of them is placed inside the thorax, with its surface opposed to the internal surfaces of the ribs. Another two ossified plates (with the same morphological characteristics cited above for the internal plates) were recovered above the sternum. Similar ossifications are also documented internally in the articulated skeletons of the Patagonian *Talenkauen* (Fig.10) and the North American *Thescelosaurus*.

Notwithstanding the fact that one plate was placed internally to the thoracic ribs, there is no evidence that it was its real position in life, because it could have been transported after the decaying process.

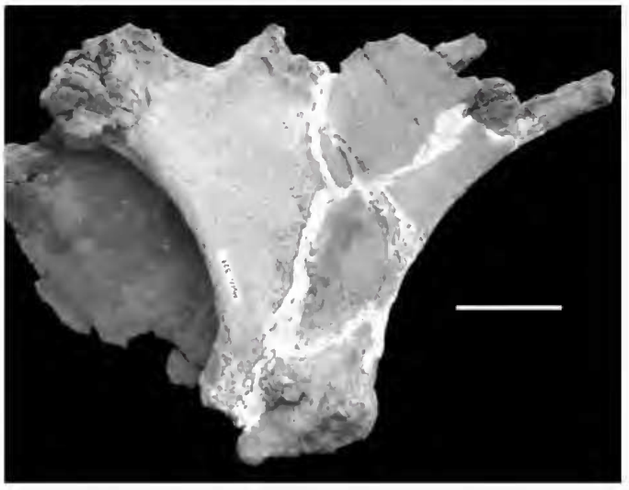
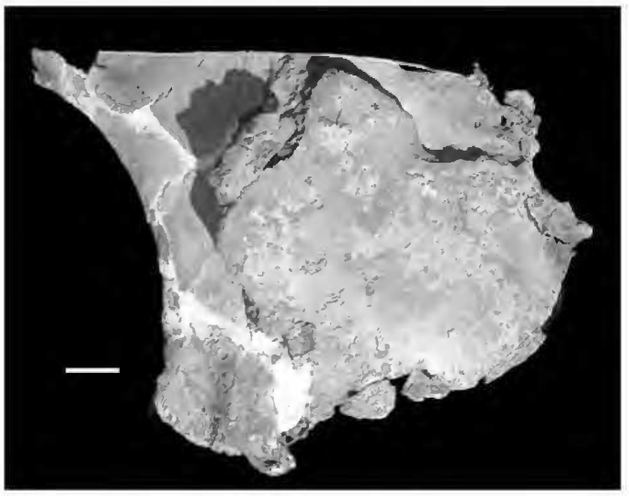


Fig.7➢
Macrogryphosaurus gondwanicus sp.nov. Thoracic plate in lateral view. Scale bar = 1cm.



➢Fig.6
Macrogryphosaurus gondwanicus sp.nov. Sternum in medial view. Scale bar = 5cm.

➢Fig.8
Macrogryphosaurus gondwanicus sp.nov. Sternum backward of behind the thoracic plate in anterior view. Scale bar = 2cm.

Pelvic Girdle and Hindlimbs

Ilium: Both ilia articulated with the sacrum were recovered (Figs.9A-9B). They are incomplete, lacking the extremities of both pre- and postacetabular processes. The left ilium lacks also the pubic peduncle. The preserved part of the preacetabular process is long and lateroventrally curved. Proximally, it is triangular incross-section, being strongly excavated on its medial side, and slightly concave on its dorsal and ventral sides. The medial surface of this process has a wide but thin horizontal ridge that serves for the attachment of the transverse processes of sacral vertebrae. The three anterior sacrals have keels and foramens as in the dorsals and anterior caudals. The dorsal edge of the ilium is slightly concave above de acetabulum and has a rugose surface. *Macrogryphosaurus* has a "S-shaped" dorsal margin of the iliac blade that is different from those present in Marginocephalia and Hypsilophodontidae, which are convex. Caudally to the acetabulum, the preserved portion of the postacetabular blade is laterally offset. This blade is not expanded dorsoventrally as that present in *Tenontosaurus* (Ostrom, 1970). The postacetabular blade is "L–shaped" in cross section, with a ventral shelf, medially projected forming an angle of more that 100 degree with respect to the axial plane) that connects with the transverse processes of the last sacral vertebra. By contrast, the brevis shelf in dryosaurids is extremely wide (Galton, 1981)

The pubic peduncle of ilium is more slender than in *Talenkauen* (Fig.9B) and the angle that it forms with the preacetabular process is less sharp (Fig.11).

Ischial and pubic peduncles are poorly developed, forming a small acetabulum. It is different from that of *Talenkauen*. The morphology of the acetabulum cavity has more resemblance with that observed in *Hypsilophodon* and *Gasparinisaura*.

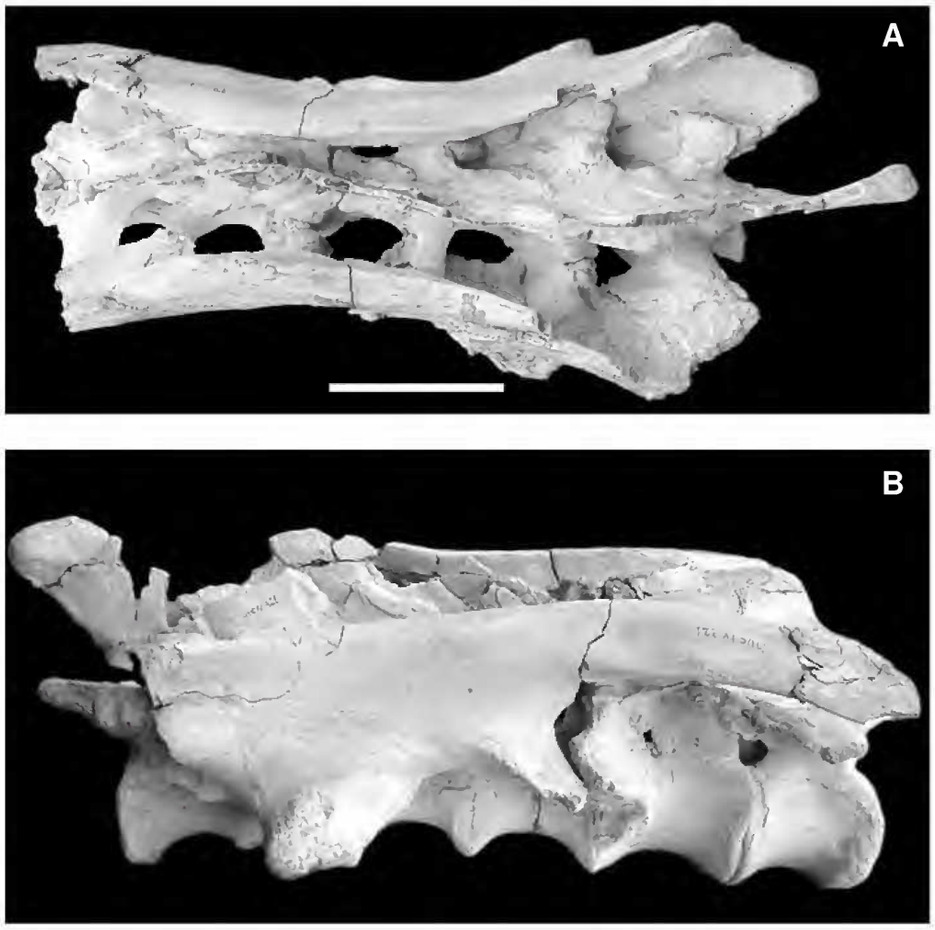


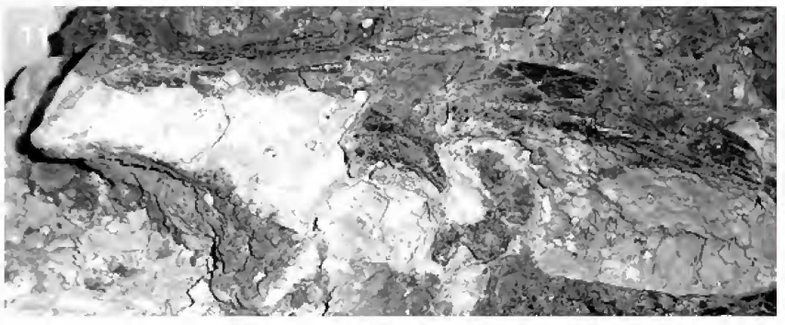
Fig.9- *Macrogryphosaurus gondwanicus* sp.nov. Sacrum, in (A) dorsal view, and (B) lateral view. Scale bar = 10cm.

The ischial peduncle has a rugose surface. It is laterally and ventrally flattened.

Ischium: Unconnected proximal, middle and distal portions of both ischia are available (Fig.12). The proximal end of ischium has two processes, one for ilium, and the other for the pubis. They are separated by a smooth acetabular embayment. The pubic process is subquadrangular in lateral view, and it ends in a flat, rectangular, rugose articular surface. The iliac process, instead, has an oval flat articular facet. The obturator process is not preserved. The ischial shaft was long, thin and curved. Taken at mid-length, the ischial shaft is twisted and has a suboval cross-section. Its distal end is slightly expanded and scarred on the medial side, indicating that left and right ischia were in contact to each other distally. Ischia bearing a small distal foot, and having a suboval or cross-section of the shaft, are also present in *Anabisetia* and Dryomorpha.

Pubis: The left pubis is almost complete (Fig.12), but the right one preserves just the pubic shaft. This bone forms the anteroventral margin of the acetabulum which is stout, concave and rugose. The prepubic process is short and flat, in contrast with the elongate and rod-like postpubic process. The length of the prepubic process is equivalent to 80% of the length of the "postpubic" process.

The presence of a higher angle (aproximatelly 150°) between pubic shaft and the prepubis is a plesiomorphic character retained in *Heterodontosaurus*. In *Macrogryphosaurus* gen.nov. this angle is lower than to 100° like that in *Camptosaurus, Thescelosaurus, Hypsilophodon, Tenontosaurus*, and *Dryosaurus*; therefore, considered a synapomorphy



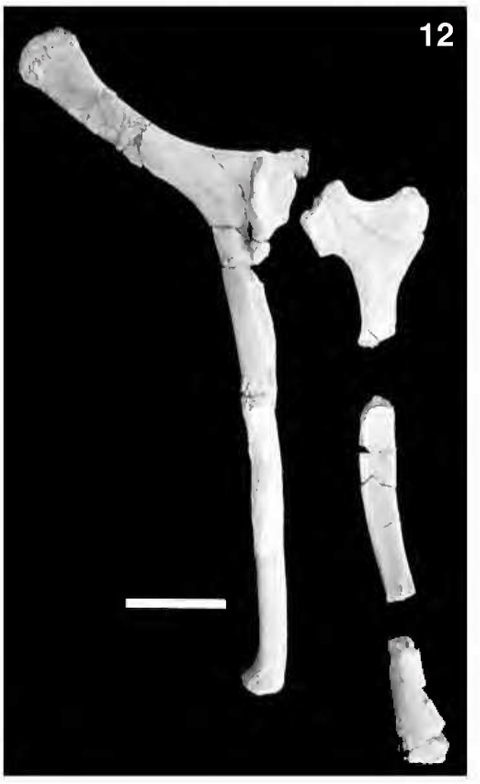


Fig.10- *Talenkauen santacrucensis*. Thoracic plate in lateral view; fig.11- *Talenkauen santacrucensis*. Ilium in lateral view; fig.12- *Macrogryphosaurus gondwanicus* sp.nov. Pubis and ischium: medial view: Scale bar = 10cm.

of Euornithopoda (Weishampel & Heinrich, 1992). The prepubic process is lateromedially compressed and expanded dorso-ventrally, with its cranial end convex and slightly expanded. In *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. the prepubis is lateromedially flat like that of *Heterodontosaurus*, *Dryosaurus*, and *Tenontosaurus*. By contrast, in *Gasparinisaura* and Hypsilophodontids, the prepubis has a rounded shape in cross section. The dorsal rim is concave in lateral view. Below the acetabulum, the postpubic process forms a narrow and curved rod. It curves backward and downward parallel to the ischium. The obturator foramen is closed, although there is a narrow notch placed dorsally. Below the obturator foramen the pubis is stout. A rugose area is developed for the attachment of the pubic head of ischium. The distal end of the pubis presents a small pubic foot resembling that of *Camptosaurus*.

DISCUSSION AND CONCLUSIONS

Cladistic analyses of ornithopods have been worked by many authors. (Sereno, 1986; Weishampel & Heinrich, 1992; Coria & Salgado, 1996; Novas *et al.*, 2004; Norman *et al.*, 2004, etc). Initially *Gasparinisaura* was considered as an Euiguanodontia (Coria & Salgado, 1996; Coria & Calvo, 2002; Novas *et al.*, 2004) but recently *Gasparinisaura* was included as a basal Ornithopoda without considering derived taxa (for instance Ankylopollexia) in the analysis (Norman *et al.*, 2004). In this paper we prefer to use a more complete analysis in order to assess the phylogenetic position of the Neuquén taxon. Therefore, we have used the comprehensive phylogenetic analysis of ornithopod relationships presented by Novas *et al.* (2004). We included the information available for *Macrogryphosaurus* gen.nov. (Fig.13) using the same data matrix from the 50 characters; we scored 14 for the new taxon (see Appendix 1). We added three new characters: (48) thin ossified plates in thoracic region; (49) third cervical with well-developed epipophyses, and (50) expanded distal end of chevron (*sensu*, Coria & Salgado, 1996).

This modified data set was run through PAUP 3.0 (DELTRAN). The resulting single tree is similar to that obtained by Novas *et al.* (2004), but two steps longer 88 steps (Fig.14). The resulting tree displayed essentially the same topology, and differed only by showing a monophyletic group formed by *Talenkauen santacrucensis* and *Macrogryphosaurus gondwanicus* gen.nov., sp.nov.; which is supported by two synapomorphies: (48) thin ossifed plates in thoracic region, and (49) third cervical with well-developed epipophyses. This new clade is named herein Elasmaria nov. The inclusion of *Macrogryphosaurus* gen.nov. in the data matrix (Novas *et al.*, 2004) improves the number of synapomorphies in Iguanodontia, adding character (22); in Euiguanodontia, adding characters (18, 26, 27), and in Dryomorpha adding characters (2, 4, 12, 19, 24, 25).

We recognize, for the first time, a Gondwanan clade of large sized basal euiguanodontians, Elasmaria nov., composed by *Talenkauen santacrucencis* and *Macrogryphosaurus gondwanicus* sp.nov..

Because the ossified plates of the thoracic region are very thin, devoid of external sculpturing; and also because they lie serially arranged on the sides of the thorax, staying connected with the caudal margin of the thoracic ribs, they were previously interpreted as uncinate processes (Novas *et al.*, 2004).

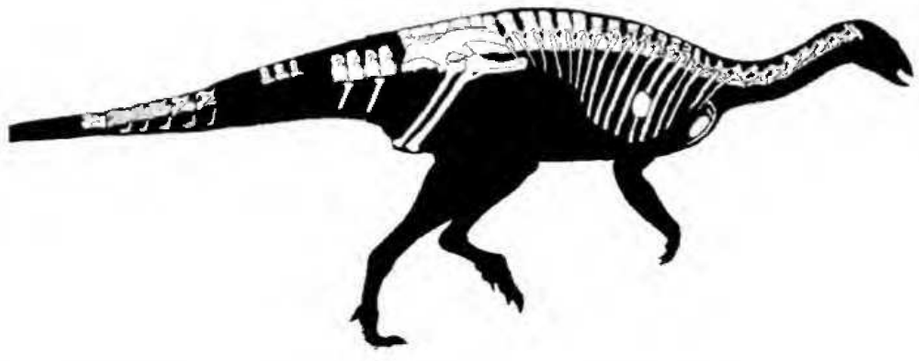


Fig.13- Reconstruction of *Macrogryphosaurus gondwanicus* sp.nov., including all preserved materials in white.

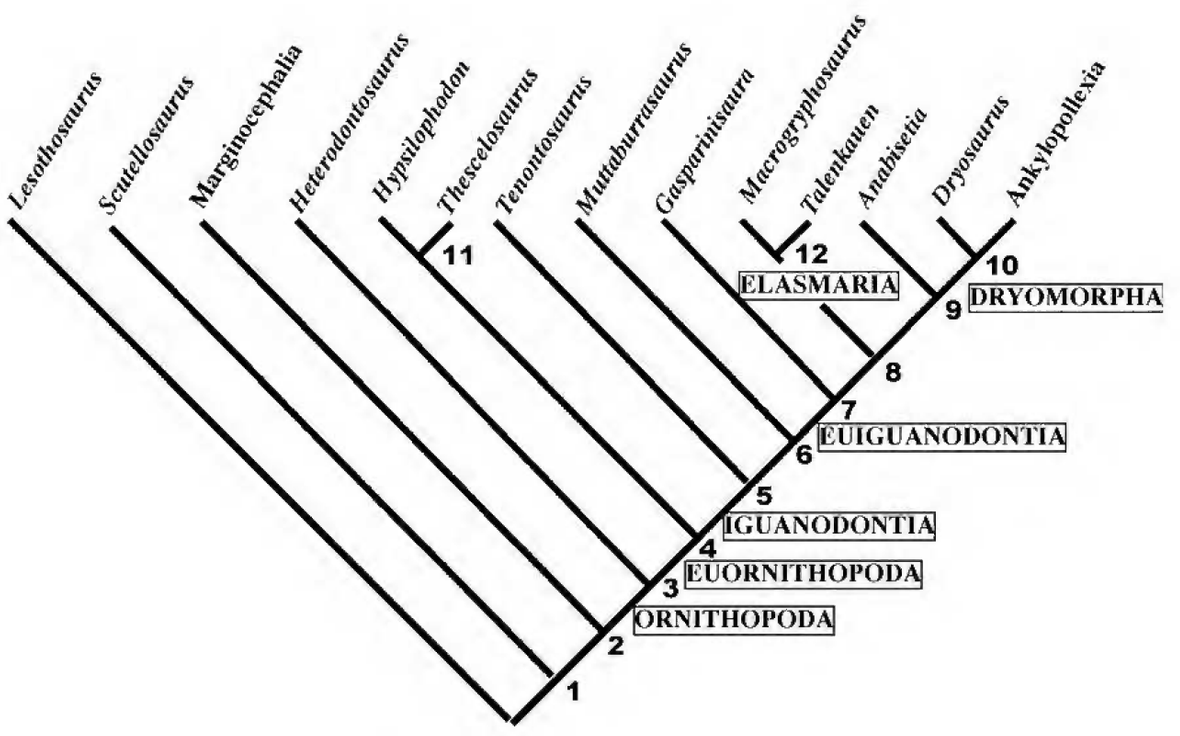


Fig.14- Cladogram depicting phylogenetic relationships of *Macrogryphosaurus gondwanicus* sp.nov. within ornithopoda, and the placement of Elasmaria. L = 88; CI = 0.625; RI = 0.742; RC = 0.463.

This made those authors hypothesize about their participation in the thoracic movements during respiration, as it occurs in living birds. These thin plates were found in *Macrogryphosaurus* gen.nov. below the thoracic ribs and between the thoracic ribs (Fig.7). Unique among Euiguanodontia, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. exhibits triradiate sternum with the anterior border tribranched, two laterally placed and outwardly directed and one smaller, centrally placed and forwardly directed. Sternal ribs flattened, twisted and distally expanded. Last dorsal with well-developed hyposphene. The thin plates plate-like located in front of the sterna. Together with these autapomorphies, this new species differs from *Talenkauen santacrucensis* by having the pubic peduncle of ilium less developed, more acute angle between the anterior process of ilium and the pubic peduncle, acetabular cavity slightly marked. Ten cervical vertebrae, 14 dorsal vertebrae, epipophyses on the 3rd cervical placed over the distal end of the postzygapophyses and posteriorly projected. Summing up, *Macrogryphosaurus gondwanicus* gen.nov., sp.nov. represents a new taxon of large sized ornithopod dinosaur from South America. It is the third example of an ornithischian dinosaur in which ossified plates on thorax are documented (Fig.10), the remaining two being the Euiguanodontia *Talenkauen santacrucensis,* from Santa Cruz and the hypsilophodontid *Thescelosaurus neglectus,* from the Maastrichtian of North America.

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APPENDIX

Character list and states were taken, with modification, from Novas *et al.* (2004). The data matrix was analyzed cladistically using the PAUP 3.0. One tree was obtained, which has the following values: L = 88; CI = 0.625; RI = 0.742; RC = 0.464.

List of Characters

1. Contact of lacrimal / premaxilla: (0) absent; (1) present.
2. Premaxillary teeth: (0) present; (1) absent.
3. Eversion of premaxilla: (0) absent; (1) present.
4. Anterior processes on maxilla: (0) 1 process; (1) 2 processes.
5. Tooth ridges connected to denticles: (0) absent; (1) present.
6. Strong central ridge on maxillary teeth: (0) absent; (1) present.
7. Denticles on predentary: (0) absent; (1) present.
8. Ventral processes on predentary: (0) single; (1) double; (2) wedge-shaped.
9. Size of antorbital fenestra or fossa: (0) large; (1) small.
10. Quadratojugal size: (0) large; (1) reduced.
11. Ossified sternal ribs: (0) absent; (1) present.
12. Ossified hypaxial tendons: (0) present; (1) absent.
13. Humerus/scapula length ratio: (0) less than 1; (1) equal or more than 1.
14. Number of phalanges on manus of digit III: (0) 4; (1) 3.
15. Number of vertebrae in sacrum: (0) 5; (1) more than 5.
16. Prepubic process: (0) absent; (1) short; (2) long rod; (3) long shallow blade; (4) deep anteriorly.
17. Femur: distal anterior intercondylar groove: (0) absent, (1) present
18. Metatarsal V/III length ratio: (0) more than 0.3; (1) less than 0.3; (2) Metatarsal-V absent.
19. Relative size of the palpebral bone: (0) 80% or more of the maximal anteroposterior width of the orbit; (1) 70% or less of the maximal anteroposterior width of the orbit.
20. Antorbital fossa shape: (0) triangular; (1) circular or ovate.
21. Dorsal and ventral margins of the dentary: (0) rostrally converged; (1) parallel.
22. Dorsal margin of iliac blade: (0) convex; (1) sinuous.
23. Size of the external nares relative to the basal skull length: (0) less than 15%; (1) 20% or more.
24. Enamel of the lingual side of maxillary teeth: (0) present; (1) absent.
25. Participation of the jugal in the antorbital fenestra: (0) included; (1) excluded.
26. Jugal-postorbital articulation: (0) medially-faced; (1) laterally-faced.
27. Brevis shelf: (0) reduced; (1) well developed.
28. Metatarsal I: (0) present; (1) reduced or absent.
29. Maxillary tooth crowns: (0) low; (1) high.
30. Foot on the distal ischial shaft: (0) absent; (1) present.
31. Ischial shaft: (0) laterally flattened; (1) suboval in cross section.
32. Caudal process of jugal: (0) well developed; (1) reduced.
33. Relative position of the ventral margin of the infratemporal fenestra: (0) below the base of the orbit; (1) above the base of the orbit.
34. Position of the obturator process on the ischial shaft: (0) proximally; (1) distally placed.
35. Deltopectoral crest, form: (0) projecting from shaft; (1) or low or rounded in lateral or medial view of the humerus.
36. Premaxilla, orientation of lower rim: (0) ventrolateral; (1) lateral.
37. Quadrate, free portion of shaft: (0) 10% or less; or (1) 30% or more of quadrate height.
38. Maxillary crowns, anteroposterior width: (0) equal; or (1) narrower than dentary crowns.
39. Maxillary crowns, shape: (0) subtriangular; (1) diamond-shaped.
40. Maxillary primary ridge strength: (0) less; or (1) more prominent than dentary primary ridge.
41. Posterior cervicals, neural spine height: (0) prominent; (1) low.

42. Cervicals 4-9, form of central surfaces: (0) slightly amphicoelous; (1) slightly opisthocoelous; or (2) strongly opisthocoelous.
43. Manual digit I-ungual, length: (0) shorter; or (1) longer than manual digit II ungual.
44. Premaxilla-maxilla diastema: (0) absent; (1) present.
45. Ischial obturator process: (0) absent; (1) present.
46. Metatarsal II transversal compression: (0) absent; (1) present.
47. Deltopectoral crest, size: (0) well developed; (1) less developed.
48. Thin ossified plates in thoracic region: (0) absent; (1) present.
49. Third cervical with well-developed epipophyses: (0) absent; (1) present
50. Chevron shape: (0) paddle-shaped; (1) flag-shaped.

Data Matrix

	5	10	15	20	25	30	35	40	45	50
Lesothosaurus	00000	00000	00000	00000	00000	00000	000?0	0000?	00?00	0000?
Scutellosaurus	00000	00000	00000	000??	00?00	00000	000?0	0000?	00000	000??
Marginocephalia	00001	10001	0?001	31000	00000	00000	000?0	00000	00000	00000
Heterodontosaurus	1000?	00200	01001	10?00	00000	00000	00000	00000	00010	00000
Talenkauen	00101	111??	??1??	3????	01?0?	??00?	????1	1?100	10?1?	1111?
Macrogryphosaurus	?????	?????	10??1	3????	?1???	?1??1	1??0?	?????	10???	??111
Thescelosaurus	?0??1	0????	10100	2010?	01?0?	?0000	01011	??000	00?11	00100
Hypsilophodon	10000	00000	10100	20010	00001	?0000	01111	00000	00111	00000
Anabisetia	????0	1????	??1??	311??	11???	?1001	1??01	???11	????1	11???
Gasparinisaura	????1	1??11	????1	20101	11??1	11100	01000	?100?	1??11	10001
Muttaburrasaurus	1???1	1??11	????1	31??1	?1101	??00?	?00?1	1000?	00?11	000??
Tenontosaurus	10100	01010	00011	31011	11111	00000	00100	10000	01011	00000
Dryosaurus	11110	11111	01011	31111	11110	11111	10001	11111	01011	00000
Ankylopollexia	11110	11111	01011	31211	11110	11111	10001	11111	12111	00000

List of Diagnostic Characters

The first number refers to the character on the list of the characters, and the derived state is given in brackets.

Ornithopoda 1 (1), 44 (1)
Euornithopoda 25 (1), 45 (1)
Iguanodontia 3 (1), 7 (1), 9 (1), 14 (1), 17 (1), 20 (1), 21 (1), 22 (1), 23 (1), 36 (1)
Euiguanodontia 18 (1), 26 (1), 27 (1), 37 (1), 41 (1), 46 (1)
Elasmaria 48 (1), 49(1)
Dryomorpha 2 (1), 4 (1), 12 (1), 19 (1), 24 (1), 25 (0), 28 (1), 29 (1), 46 (0)